An unusual small-bodied crocodyliform from the Middle Jurassic of Scotland, UK, and potential evidence for an early diversification of advanced neosuchians

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ABSTRACT: The Middle Jurassic is a poorly sampled time interval for non-pelagic neosuchian crocodyliforms, which obscures our understanding of the origin and early evolution of major clades. Here we report a lower jaw from the Middle Jurassic (Bathonian) Duntulm Formation of the Isle of Skye, Scotland, UK, which consists of an isolated and incomplete left dentary and part of the splenial. Morphologically, the Skye specimen closely resembles the Cretaceous neosuchians *Pachycheilosuchus* and *Pietraroiasuchus*, in having a proportionally short mandibular symphysis, shallow dentary alveoli and inferred weakly heterodont dentition. It differs from other crocodyliforms in that the Meckelian canal is dorsoventrally expanded posterior to the mandibular symphysis and drastically constricted at the 7th alveolus. The new specimen, together with the presence of *Theriosuchus* sp. from the Valtos Formation and indeterminate neosuchians from the Kilmaluag Formation, indicates the presence of a previously unrecognised, diverse crocodyliform fauna in the Middle Jurassic of Skye, and Europe more generally. Small-bodied neosuchians were present, and ecologically and taxonomically diverse, in nearshore environments in the Middle Jurassic of the UK.

KEY WORDS: Crocodyliformes, Duntulm Formation, Isle of Skye, Neosuchia

Modern crocodiles, caiman, gharials and alligators are the only living members of Crocodyliformes, a group of pseudosuchian archosaurs whose evolutionary history spans about 200 million years (Whetstone & Whybrow 1983; Benton & Clark 1988; Bronzati *et al*. 2015; Mannion *et al.* 2015). The Middle Jurassic was a key period in their evolution, with thalattosuchians rapidly diversifying in the marine realm (e.g., Gasparini and Chong 1977; Young *et al.* 2010, 2011; Wilberg 2015). However, much less is known about the non-pelagic crocodyliforms from this time. Apparently, terrestrial and freshwater species were stuck in a low point of their diversity, although this could be an artefact of the notoriously poor Middle Jurassic tetrapod fossil record (Tennant *et al.* 2016a). Sparse sampling during this interval complicates our understanding of the diversification patterns of non-pelagic crocodyliforms (Bronzati *et al.* 2015; Mannion *et al.* 2015; Tennant *et al.* 2016b), meaning that new Middle Jurassic fossils are critical.

Indeed, crocodyliforms from terrestrial and nearshore assemblages during the Middle Jurassic remain poorly understood compared with those from other geological intervals. During the Late Jurassic, most non-pelagic crocodyliforms in Europe were gonio-pholidids and atoposaurids (Andrade *et al.* 2011; Young *et al.* 2016a; Tennant *et al.* 2016b, c), whereas in other parts of the world, small-bodied sphenosuchian and protosuchian-grade taxa were widely distributed (Gao 2001; Clark *et al.* 2004; Göhlich *et al.* 2005; Pol *et al.* 2013). By the Early Cretaceous, European faunas were composed of a more diverse assemblage of neosuchians, including goniopholidids, pholidosaurids, bernissartiids, putative atoposaurids and hylaeochampsids (e.g., Salisbury & Naish 2011; Sweetman *et al.* 2015). Ghost lineage analyses imply that, depending on the systematic position of the Cretaceous clades, some major neosuchian lineages may have originated during the dark period of the Middle Jurassic (e.g., Bernissartiidae, Hylaeochampsidae, Paralligatoridae and Pholidosauridae: Bronzati *et al.* 2015; Turner 2015; Tennant *et al.* 2016b).

The problem, however, is that there are currently few known places where Middle Jurassic, non-pelagic crocodyliforms can be found. Jurassic fossil-bearing beds of terrestrial, freshwater and lagoonal origins are sparsely distributed in China (Gao 2001; Maisch *et al.* 2003; Fu *et al.* 2005), Kyrgyzstan (Averianov 2000), parts of Europe (Evans & Milner 1994; Kriwet *et al.*
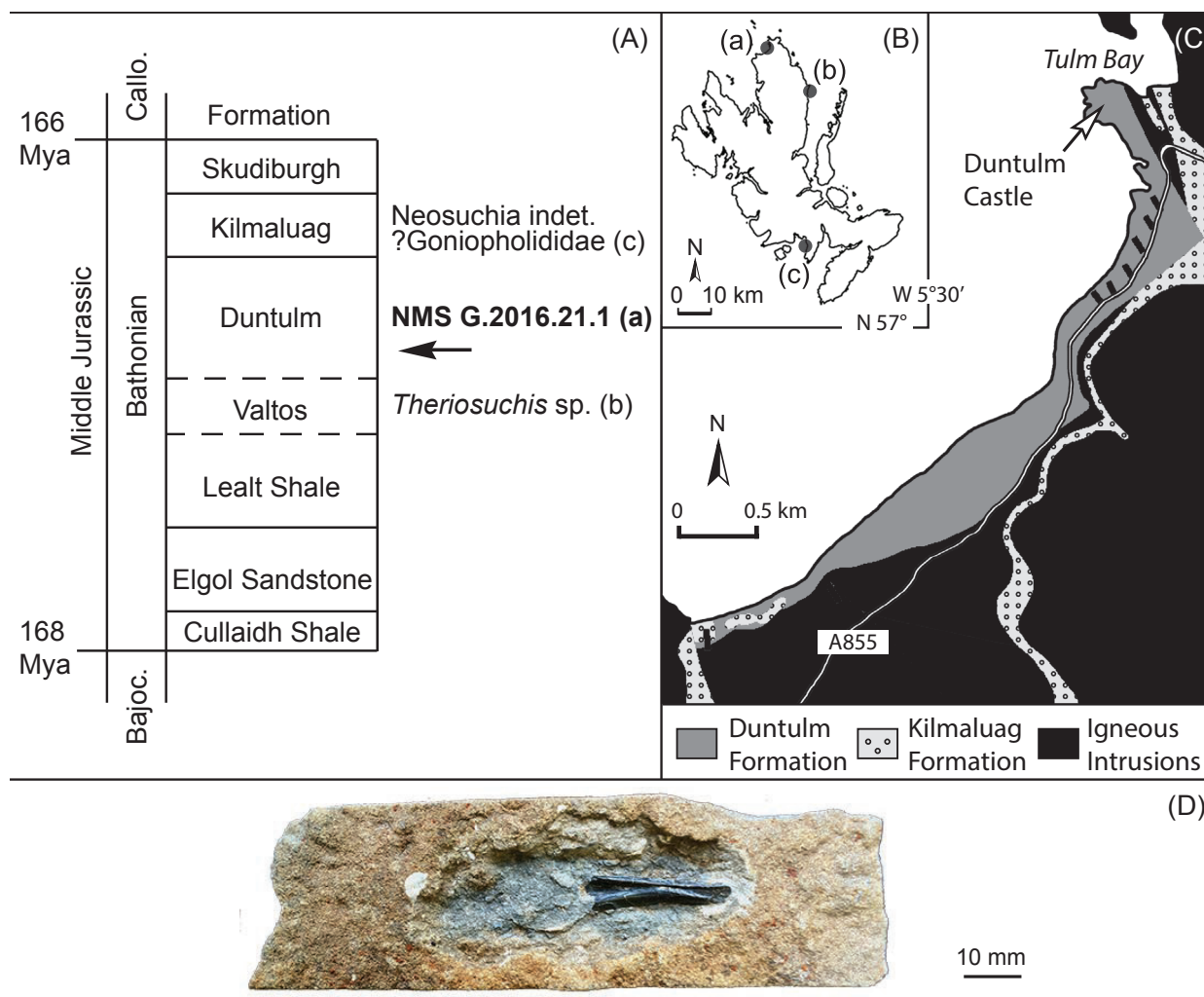
Figure 1 Locality and geological context of NMS G.2016.21.1: (A) stratigraphic occurrences of fossil crocodyliforms discovered from the Great Estuarine Group; (B) map of the Isle of Skye, showing three localities of known fossil crocodyliforms: (a) = Duntulm; (b) = Valtos; (c) = Cladach a'Ghlinne; (C) geological context at the Duntulm locality (a); (D) the new specimen NMS G.2016.21.1.

1997; Knoll *et al.* 2013; Knoll & López-Antoñanzas 2014; Young *et al.* 2016a) and Russia (Kuzmin *et al.* 2013), which has yielded some crocodyliform fossils. Furthermore, there are undescribed crocodyliform teeth of this age from Thailand (Tong *et al.* 2002) and possible remains from Madagascar (Dal Sasso & Pasini 2003; Flynn *et al.* 2006), but these are fragmentary. The vast majority of Middle Jurassic crocodyliform fossils are isolated specimens from microvertebrate localities – limited evidence that makes it difficult to assign these fossils to higher-level clades, which in turn hinders our understanding of the origin and early evolution of these groups that would later go on to great diversity and success in the Cretaceous and beyond.

Here we report a new crocodyliform lower jaw from the Middle Jurassic of the Isle of Skye, Scotland, UK (Fig. 1). This study is part of an ongoing investigation of the world-class Middle Jurassic vertebrate fossil record of Skye, led by the PalAlba Group (Brusatte *et al.* 2015, 2016; Brusatte & Clark 2015; Young *et al.* 2016a). Previously identified crocodyliforms from Skye include indeterminate remains (Evans *et al.* 2006; Wills *et al.* 2014) and a partial skeleton (Evans & Waldman 1996) from Cladach a'Ghlinne (Fig. 1B) and, most recently, a partial lower jaw assigned to *Theriosuchis* sp. (Young *et al.* 2016a) from Valtos (Fig. 1B). The new specimen here represents a hitherto unknown small-bodied taxon from the Middle Jurassic Skye tetrapod assemblage, and has impli-

cations for the diversity and ecology of non-pelagic crocodyliforms of the poorly-sampled Middle Jurassic.

Note, that herein we use the term Hylaeochampsidae in a broad sense, referring to taxa previously referred to Hylaeochampsidae (compare this clade's taxonomic composition in Buscalioni *et al.* 2011; Puértolas-Pascual *et al.* 2014; Narváez *et al.* 2015; Turner 2015; Schwarz *et al.* 2017). We use the term 'putative hylaeochampsid' for species with no consensus on their phylogenetic position; i.e., *Pachycheilosuchus trinquei* Rogers, 2003 and *Pietraroiasuchus ormezzanoi* Buscalioni *et al.*, 2011, as some phylogenetic analyses fail to recover them within Hylaeochampsidae or within a derived neosuchians position (e.g., Narváez *et al.* 2015; Tennant *et al.* 2016c). In addition, a recent study using the Turner (2015) matrix recovered the susisuchids *Susisuchus* and *Isisfordia* to be paraphyletic, and both to be within Hylaeochampsidae *sensu lato* (Schwarz *et al.* 2017), highlighting the uncertainty in the taxonomic composition of this clade at present.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; IPFUB, Institut für Paläontologie der Freie Universität Berlin, Berlin, Germany; NHMUK, Natural History Museum, London, UK; NMS, National Museums Scotland, Edinburgh, UK; PC-1, provisional specimen number for *Pietraroiasuchus ormezzanoi* Buscalioni *et al.*, 2011 at Museo Regionale di Scienze Naturali di Torino,

Italy; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.

1. Systematic Palaeontology

Crocodyliformes Benton & Clark, 1988
Mesoeucrocodylia Whetstone & Whybrow, 1983
Neosuchia Benton & Clark, 1988
Neosuchia *cf*. Hylaeochampsidae

Specimen. NMS G.2016.21.1: an isolated and incomplete, three-dimensionally preserved left lower jaw, including much of the dentary and part of the splenial. The specimen preserves the complete anterior margin of the dentary, but it is broken posteriorly at the 14th alveolus.

Possible unity with hylaeochampsids. Neosuchia *cf*. Hylaeochampsidae (NMS G.2016.21.1) resembles the putative hylaeochampsids *Pachycheilosuchus* and *Pietraroiasuchus* in having shallow dentary alveoli, mildly heterodont dentition and a proportionally short mandibular symphysis extending to the anterior border of the 4th alveolus.

Differential diagnosis. NMS G.2016.21.1 differs from other neosuchians in having an extremely reduced lingual projection along the mandibular symphyseal suture and in having neurovascular foramina present medial to the tooth row, with a one-to-one association with the tooth sockets from alveoli 5–9. NMS G.2016.21.1 differs from *Pachycheilosuchus* in having a Meckelian canal that is markedly constricted at the 7th alveolus, and it differs from *Pietraroiasuchus* in having dentary alveoli that are tightly arranged. Furthermore, the new specimen (NMS G.2016.21.1) differs from all other hylaeochampsids in that its 6th dentary alveolus is smaller than the 5th and 7th and slightly raised from the tooth row.

Locality. The specimen was collected from bed 46 of the type section of the Duntulm Formation at the southern part of the exposures [NG407 734] at Cairidh Ghlumaig, Isle of Skye, Scotland, United Kingdom (Morton & Hudson 1995, figs 35–36, table 2; Fig. 1C).

The Duntulm Formation (Bathonian, Middle Jurassic) is part of the Great Estuarine Group, (Anderson 1948), which crops out in portions of the northwest Highlands of Scotland, including the Isles of Skye, Raasay, Eigg and Muck (Harris & Hudson 1980). It consists of sedimentary rocks of marginal marine and non-marine origin, deposited in the Hebrides Basin during the Bathonian of the Middle Jurassic (Harris & Hudson 1980).

Seven formations belong to the Great Estuarine Group (Fig. 1A). The upper formations of the Group, following an initial transgression across the fluvial deltas of the Valtos Formation, were deposited during a phase of marine regression (Andrews 1985). It shows a transition from shelly limestone, shale and mudstone in the Duntulm Formation (Andrews & Walton 1990), to interbedded shale, fine-grained limestone and dolomite (with desiccation cracks) and fine-grained sandstones in the freshwater lagoonal Kilmaluag Formation and, finally, to silty clay, coarse sandstone and intraformational conglomerates in the fluvial Skudiburgh Formation (Andrews 1985).

The Duntulm Formation represents the nearest approach to marine conditions within the Great Estuarine Group. The strata from which NMS G.2016.21.1 was collected have one of the most marine-dominated molluscan faunas within the Duntulm Formation as a whole. In these beds, the small oyster *Praeexogyra*, which forms nearly monotypic shell beds that dominate much of the formation, is joined by bivalve genera such as *Camptonectes*, *Placunopsis*, *Corbula* and *Modiolus*, and by echinoid spines, all indicative of shallow marine environment

(Andrews & Walton 1990). The trace fossil *Thalassinoides* indicates the presence of burrowing crustaceans (Myrow 1995).

With that said, the Duntulm facies are not simply marine. Cyanobacterial ('algal') limestones interbedded with the oyster-bearing limestones show evidence of both subaerial exposure and freshwater flushing (Andrews 1986). Carbon, oxygen and strontium isotopic studies of the oysters show that the lagoons where they lived were at times isolated from the sea and suffered evaporation (Holmden & Hudson 2003). An intercalation of strata bearing the bivalves *Unio* and *Neomiodon*, a few metres above where NMS G.2016.21.1 was discovered, emphasises the potential for freshwater input, confirmed by the isotopic investigations. A scenario depicting the overall environment was presented by Hudson & Trewin (2003). Dinosaur fossils, most notably the trackways of large sauropods, are now known from the lower part of the formation (Brusatte *et al.* 2016), northeast of where NMS G.2016.21.1 was collected.

Bed 46, from which the crocodyliform specimen came, is sandier than the surrounding beds. Unlike them, it yields the freshwater alga *Bothrococcus*, probably washed in along with the sand (Andrews & Walton 1990). In NMS G.2016.21.1, the matrix surrounding the bone is greenish grey sandstone that weathers to a buff-orange colour (Fig. 1D). Besides the crocodyliform jaw, the matrix preserves fish scales, fish teeth and shells of the oyster *Praeexogyra*. The small oysters are preserved isolated and broken, confirming a high-energy near-shore environment. It is possible that the crocodyliform jaw was washed in; however, given that the dominant fauna of bed 46 is of marine-related genera, we consider NMS G.2016.21.1 most likely to have been a lagoonal species.

Preparation and scanning. Physical preparation exposed the medial surface of the jaw and most of the dorsal surface of the tooth row, whereas the lateral surface and the anterior tip of the dentary remain embedded within the matrix (Fig. 1D). We used high-resolution X-ray computed tomography (HRCT) to visualise the entire specimen, including the embedded portions (Fig. 2). We scanned the fossil in a custom-built machine (constructed and operated by Dr Ian Butler) at the School of GeoSciences, University of Edinburgh, using a 240 kv GE X-ray generator. The scan has a resolution of 44 μm, which was performed under 2.8 w power and with a 0.8 mm Aluminium filter.

2. Description

The preserved lower jaw shows no obvious taphonomic distortion or post-mortem damage, apart from the break at the posterior end. The specimen is laterally compressed, measuring 28 mm anteroposteriorly, 6 mm dorsoventrally at the deepest point and less than 4 mm labiolingually (Fig. 2). The posterior margin terminates at the 14th dentary alveolus (D14); therefore, we cannot assess the total number of dentary teeth (Fig. 2A–B). The irregular shape of this posterior margin suggests it represents a fracture, rather than the anterior margin of the external mandibular fenestra. This means that the specimen preserves the anterior part of the left dentary and a small fragment of the splenial (Fig. 2E–H). The angular and surangular are not preserved, and we cannot determine whether a mandibular fenestra was present.

2.1. Dentary

In dorsal view, the dental arcade occupies almost the entire mediolateral width of the occlusal surface of the lower jaw. The anterior tooth row has a medial ridge extending between the 2nd and 9th alveoli (D2–D9), which provides an elongate articulation surface for the splenial. We estimate that the splenial extended as far anteriorly as the anterior border of
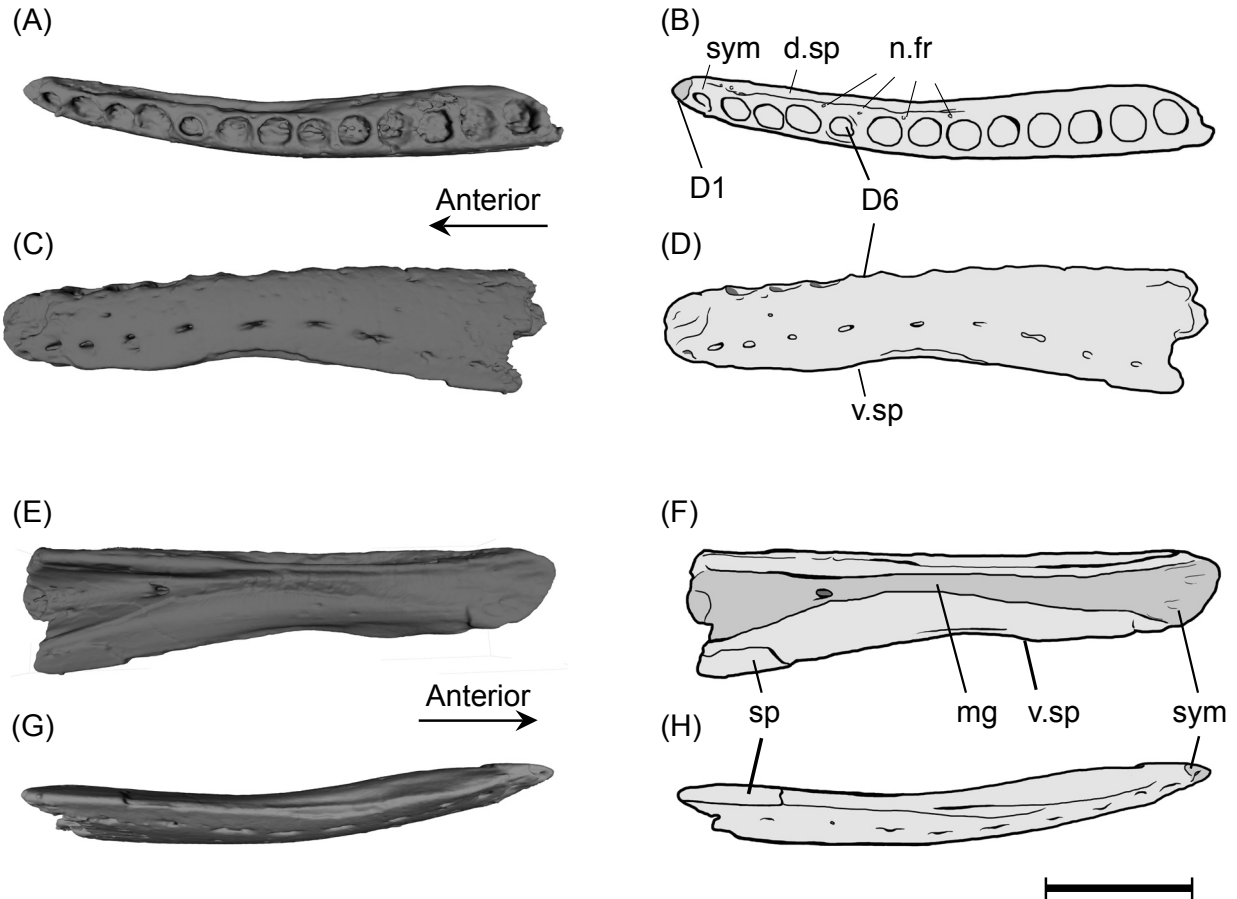
Figure 2 CT models and line drawings of specimen NMS G.2016.21.1: (A–B) dorsal view; (C–D) lateral view; (E–F) medial view; (G–H) ventral view. Anatomical abbreviations: D1 = first dentary tooth; D6 = sixth dentary tooth; d.sp = dentary articulation surface for the splenial; mg = Meckelian groove; n. fr = neurovascular foramina; sp = splenial; sym = mandibular symphysis; v.sp = ventral articulation surface for the splenial. Scale bar = 10 mm.
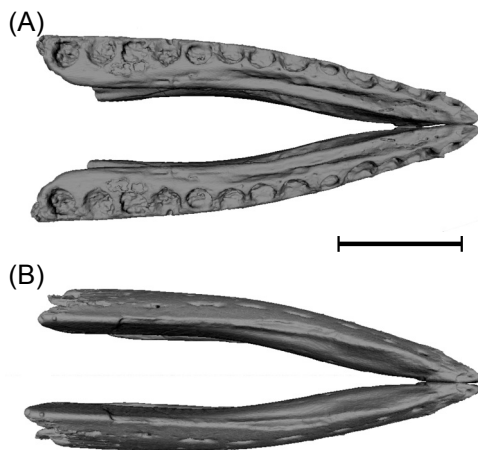

Figure 3 Reconstructed CT models of the anterior mandibles of NMS G.2016.21.1: (A) dorsal view; (B) ventral view. Scale bar = 10 mm.

the 6th alveolus (Fig. 2: v.sp). Neurovascular foramina are present medial to the tooth row. Anterior to the 5th alveolus (D5), these foramina are irregularly distributed. From D5 to D9, one foramen is located posterior to each alveolus in the raised tooth row (Fig. 2B).

In lateral view, the dentary has a straight dorsal margin and a concave ventral margin. It gradually tapers dorsoventrally towards the anterior tip and medially into the symphysis (Fig. 2C–D). A series of ten evenly-spaced neurovascular foramina occupy the lateral external surface of the bone. The row of foramina follows the curvature of the ventral margin of the dentary.

Medially, the mandibular symphysis fully occupies the anterior tip of the dentary. The symphysis is anteroposteriorly short in proportion to the dentary, ending at the anterior border of the 4th alveolus (D4). The symphyseal surface bears longitudinal striations for articulation, distinct from deep rugosities in many mesoeucrocodylians (Holliday & Nesbitt 2013). The Meckelian canal enters the symphyseal plate anteriorly and continues along the entire length of the preserved dentary. It shows a distinct dorsoventral constriction at the 7th alveolus (D7), followed by a trumpet-shaped expansion that opens to the truncated posterior margin of the specimen. A large neurovascular foramen is located in the Meckelian canal posterior to the constricted area, beneath the 11th alveolus (D11). A small fragment of splenial is preserved at the posteroventral margin of the dentary, and the splenial does not appear to have contributed to the symphysis (Fig. 2).

The ventral profile of the dentary is labiolingually narrow. The dentary curves towards the midline of the skull from the 6th alveolus (D6) to the anterior tip (Fig. 2A–B, G–H). We digitally mirrored the specimen to reconstruct a composite full lower jaw for NMS G.2016.21.1. The reconstructed mandibles display a tapering tip at the symphysis (Fig. 3), compared with the more rounded or U-shape outline in most crocodyliforms (Romer 1956).
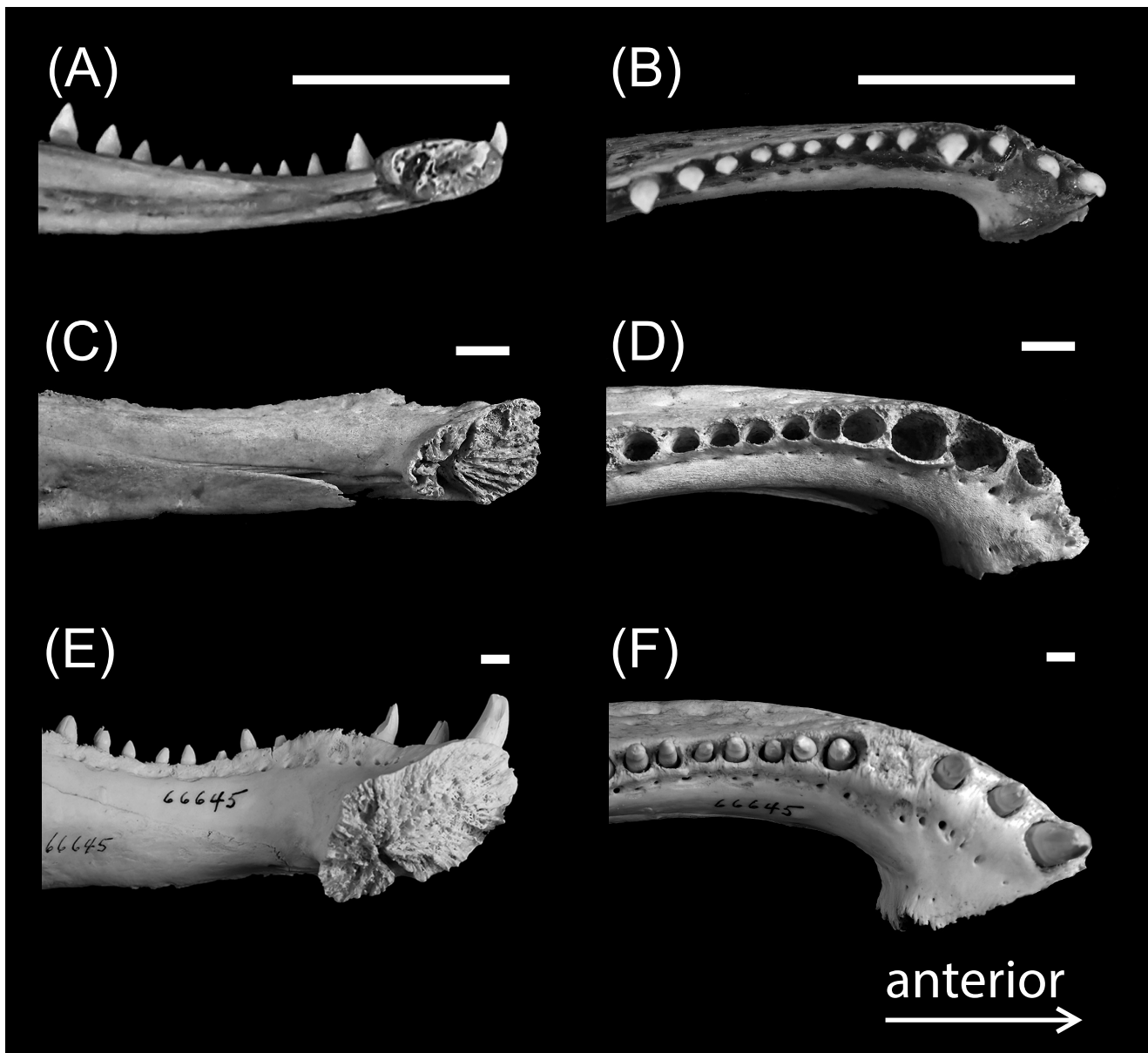
Figure 4 The mandibular symphysis of *Alligator mississippiensis* through ontogeny: (A–B) left mandibular rami of a hatchling (AMNH R7129): (A) medial view; (B) dorsal view; (C–D) a medium-sized individual (AMNH R7140): (C) medial view; (D) dorsal view; (E–F) an adult (AMNH R66645): (E) medial view; (F) dorsal view. Scale bars = 10 mm.

2.2. Alveoli

The dentary preserves 14 alveoli, but no teeth are preserved fully or partially *in situ*, nor are any associated tooth crowns present within the surrounding matrix. The first five alveoli (D1–D5) are longitudinally elongated and labiolingually compressed, whereas the posterior alveoli (D6–D14) are round. No caniniform tooth is observed in the specimen. Most of the alveoli measure approximately 1.5 mm in diameter, with the 1st, 2nd and 6th alveoli being about half the size of adjacent ones (Fig. 2A–B). Therefore, we infer that the lower jaw dentition was mildly heterodont, with two tooth "waves". Each alveolus is separated by an interalveolar septum; the first two septa and those posterior to D6 are approximately uniform in width, but those between D3–D5 are almost absent. The septa surrounding the 6th alveolus (D6) are marginally wider, as this alveolus is slightly raised from the tooth row. The preserved alveoli are shallow, extending no deeper than the dorsal margin of the Meckelian canal.

2.3. Developmental stage

With 14 alveoli, the preserved portion of the dentary measures 28 mm (D1–D14). A row of the same number of dentary alveoli measures 30 mm in *Knoetschkesuchus* (IPFUB Gui Croc 8109: Schwarz & Salisbury 2005; Schwarz *et al.* 2017), 40–45 mm in *Pachycheilosuchus* (SMU 75278: Rogers 2003) and *Pietraroiasuchus* (PC-1: Buscalioni *et al.* 2011), and about 65 mm in *Goniopholis* (NHMUK PV OR 48300: Salisbury 2002), which are small-bodied neosuchians, all appearing to be represented by anatomically mature specimens. Therefore, NMS G.2016.21.1 is smaller than an adult, and generally matches the size of a sub-adult or juvenile, when compared with the above taxa. When compared with the extant crocodylian *Alligator mississippiensis* Daudin, 1802 (a medium-large bodied eusuchian), NMS G.2016.21.1 is equivalent to a hatchling in size (Fig. 4). Future discoveries of fossil material may help better assess the developmental stage of this new Skye specimen.

3. Crocodyliform affinity of NMS G.2016.21.1

The Middle Jurassic of the Isle of Skye yields a diverse array of archosaurs, lepidosaurs, choristoderes, stem mammals and marine reptiles (e.g., Waldman & Savage 1972; Clark *et al.* 1995; Evans & Waldman 1996; Evans *et al.* 2006; Wills *et al.* 2014; Brusatte *et al.* 2015, 2016; Brusatte & Clark 2015; Close *et al.* 2016; Young *et al.* 2016a). NMS G.2016.21.1 differs from lepidosaurs and choristoderes in having thecodont dentition with rounded alveoli and a single row of neurovascular foramina on the lateral surface (Romer 1956; Gao & Fox 1998). It also differs from ichthyosaurs in having shallow tooth sockets: some Triassic ichthyosaurian taxa have thecodont dentition, but their tooth roots attach deeply in the jaw bones (Motani 1997). The dentary of NMS G.2016.21.1 lacks tooth replacement pits, which contrasts with the multiple rows of dentary teeth in eosauropterygians (Sassoon *et al.* 2015). Amongst archosaurs, NMS G.2016.21.1 differs from dinosaurs in having the long Meckelian canal extending into the mandibular symphysis (Romer 1956; Holliday & Nesbitt 2013). A pterosaur affinity is unlikely, as they generally have elongate mandibular symphysis (Romer 1956).

Crocodyliforms and some derived "sphenosuchians" have the Meckelian canal extending into the mandibular symphysis (Nesbitt 2011), which is the same as in NMS G.2016.21.1. However, "sphenosuchians" have a proportionally longer mandibular symphysis than the new specimen (Colbert & Mook 1951; Clark & Sues 2002; Clark *et al.* 2004; Pol *et al.* 2004). In non-crocodyliform diapsids, the neurovascular foramina are limited to a single line near the dorsal margin of the dentary, whereas in crocodyliforms the neurovascular foramina are more numerous and form a "beehive" arrangement, which is associated with the presence of dome pressure receptors (Soares 2002). The arrangement of dentary foramina in NMS G.2016.21.1 is consistent with those of crocodyliforms (Soares 2002). Therefore, we exclude NMS G.2016.21.1 from these other groups, and confidently refer it to a small-bodied, juvenile to sub-adult crocodyliform.

4. Taxonomic comparisons within Crocodyliformes

As mentioned previously, there is a diverse range of Middle Jurassic crocodyliform clades either known from fossils or inferred from ghost lineages to which NMS G2016.21.1 could potentially be assigned. Here, we provide extensive comparisons to all clades as a process of elimination to deduce a likely candidate clade for the specimen.

The new specimen (NMS G2016.21.1) has a short mandibular symphysis, shallow dentary alveoli and inconspicuous dentary ornamentation. It differs from large-bodied aquatic clades that evolved elongate symphyseal sutures and lower jaws, such as Thalattosuchia, the most commonly discovered and diverse Middle Jurassic crocodyliforms (e.g., Andrews 1913; Pierce & Benton 2006; Young *et al.* 2010). Among taxa considered to be "protosuchians", species with a similarly short mandibular symphyseal suture have markedly different dentary morphology when compared with the new specimen. *Zosuchus davidsoni* Pol & Norell, 2004a and *Gobiosuchus kielanae* Osmólska, 1972 are labiolingually expanded at the anterior tip of the dentary (Osmólska *et al.* 1997; Pol & Norell 2004a), whereas NMS G.2016.21.1 is labiolingually compressed along the symphyseal suture. Numerous notosuchian genera have anteriorly tapering mandibles with short symphyses, including *Araripesuchus* (Pol & Apesteguía 2005; Turner 2006), *Notosuchus* (Fiorelli & Calvo 2008), and *Malawisuchus* (Gomani 1997). However, the dentary of notosuchians is much more sigmoid than in
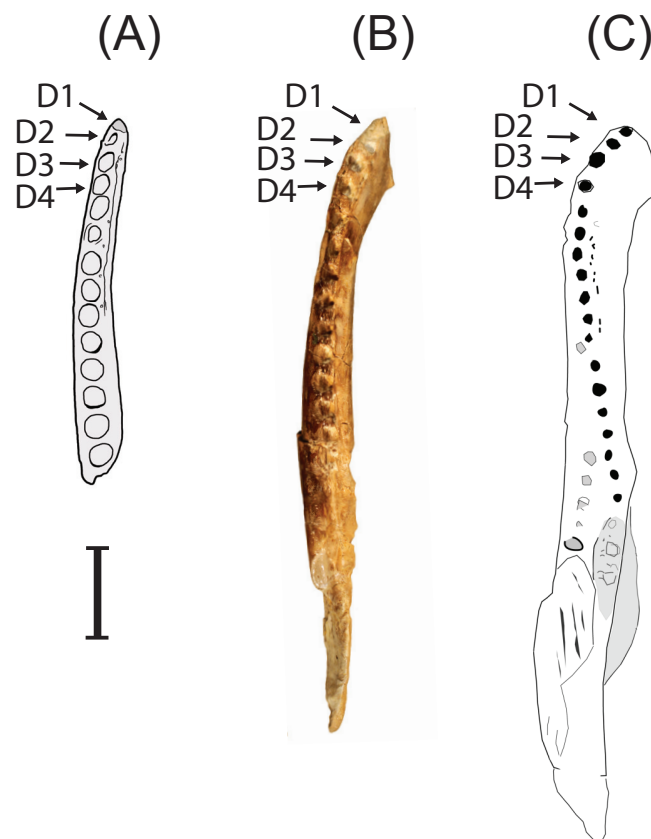

Figure 5 Lower jaw comparisons between NMS G.2016.21.1 and Early Cretaceous hylaeochampsids: (A) the Duntulm specimen (NMS G.2016.21.1); (B) *Pachycheilosuchus trinquei* (SMU75279). Photograph by D. Winkler; (C) *Pietraroiasuchus ormezzanoi* (PC-1, modified from Buscalioni *et al.* 2011). D1–D4 denotes first four alveoli.

NMS G.2016.21.1. Therefore, we consider the referral of NMS G.2016.21.1 to Notosuchia to be unlikely.

The new specimen (NMS G.2016.21.1) also differs from several small-bodied "atoposaurids" known from the UK and across Europe. *Theriosuchus* sp. from the Middle Jurassic of Skye (Tennant *et al.* 2016c; Young *et al.* 2016a) has deeper rugosities in the symphyseal plate, more prominent ornamentation on the lateral surface of the dentary and a different alveolar morphology. Compared with NMS G.2016.21.1, *Alligatorium* has a curved dorsal margin of the dentary, and *Atoposaurus* and *Alligatorellus* have the splenial contributing to the mandibular symphysis; although the latter two most likely represent skeletally immature specimens (Tennant & Mannion 2014; Tennant *et al.* 2016c). *Montsecosuchus*, a small-bodied, phylogenetically uncertain neosuchian from Spain (Buscalioni & Sanz 1990; Tennant *et al.* 2016c), has more strongly developed dentary ornamentation than NMS G.2016.21.1.

The Skye jaw (NMS G.2016.21.1) differs from genera consistently found to be hylaeochampsids. Recent analyses that gave conflicting evolutionary positions for the putative hylaeochampsid *Pachycheilosuchus* do not do so for *Acynodon* or *Iharkutosuchus*, instead consistently recovering them within Hylaeochampsidae (e.g., Turner 2015; Narváez *et al.* 2015; Schwarz *et al.* 2017). *Acynodon*, although originally described as being more closely related to crocodylians, is known from the Late Cretaceous of Europe, and includes preserved dentary material for multiple specimens (Delfino *et al.* 2008a; Martin 2007). However, *Acynodon* differs from NMS G.2016.21.1 in the vast stratigraphic range disparity, as well as in multiple dentary characteristics: the symphysis extends more than four
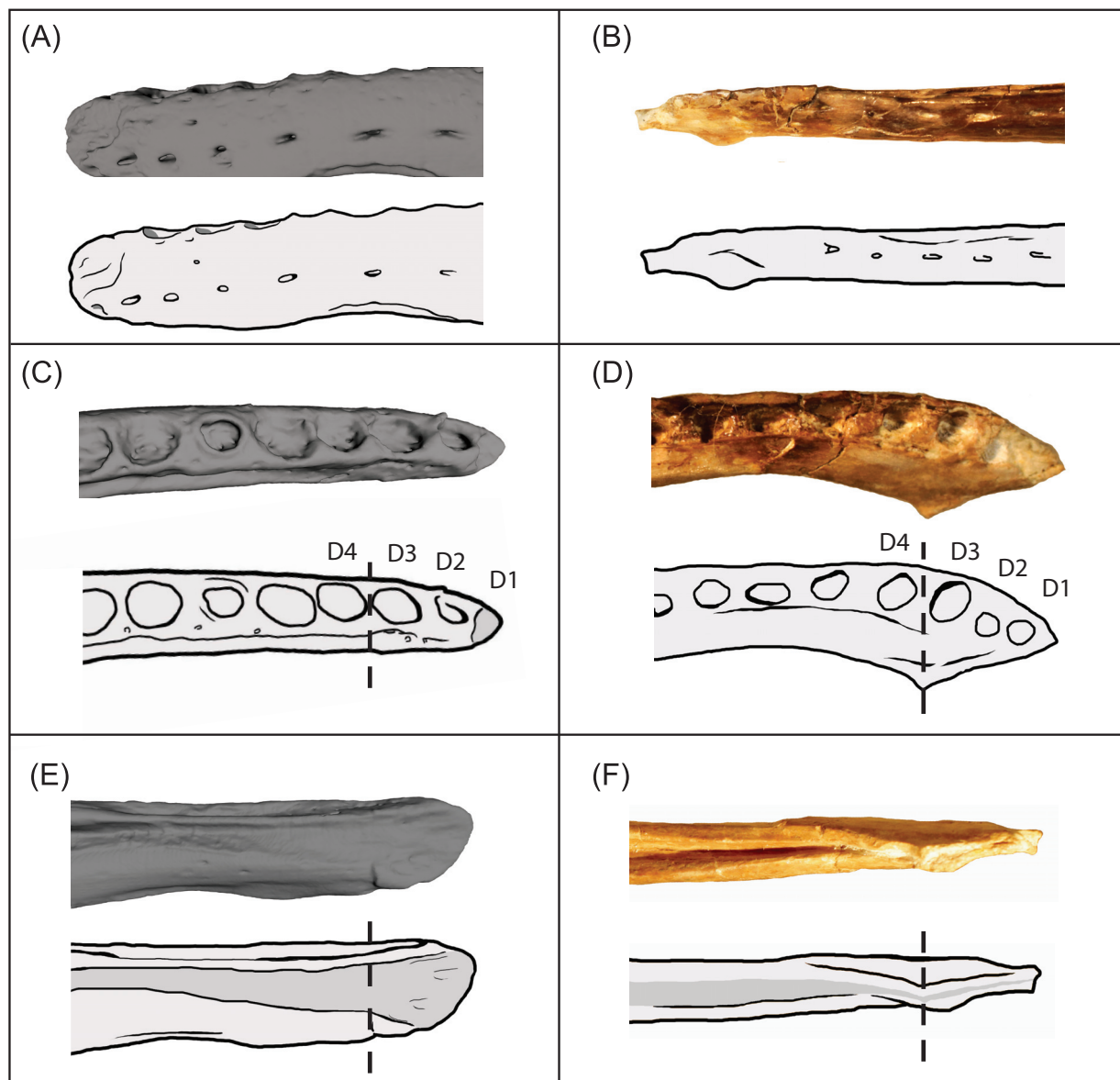
Figure 6 Morphological comparisons between NMS G.2016.21.1 (A, C, E) and *Pachycheilosuchus trinquei* (SMU75279: B, D, F): (A–B) dentary in lateral view. A row of neurovascular foramina evenly distributes along the lateroventral margin in both taxa; (C–D) dentary in dorsal view. D1–D4 denotes first four alveoli; (E–F) the Meckelian canal expands dorsoventrally in the new specimen, but constricts anteriorly in *P. trinquei*. Dashed lines indicate the posterior limit of the symphyseal plate. Not to scale.

alveoli, the dentary alveoli form a chain and are small and laterally placed relative to the dorsal surface and the ventral surface is greatly mediolaterally expanded and flattened (Delfino *et al.* 2008a; Martin 2007). The dentary of *Iharkutosuchus* is distinct from NMS G.2016.21.1 in that the symphysis extends posteriorly to the D8 alveolus, and in that the dental arcade forms an arcuate shape, shifts posteriorly from a lateral position to a more medial position on the occlusal surface, and has a mediolaterally expanded anterior margin similar to other eusuchians (Ősi 2008). Unfortunately, the type species *Hylaeochampsa vectiana* Owen, 1874 does not preserve the dentary (Clark & Norell 1992). Similarly, comparison with *Allodaposuchus*, a possible Late Cretaceous allodaposuchid or putative hylaeochampsid, depending on analysis used (see Buscalioni *et al.* 2011; Delfino *et al.* 2008b; Puértolas-Pascual *et al.* 2014; Narváez *et al.* 2015), is not possible, as no known specimen preserves the dentary. A recent study extending the Turner (2015) analysis found the susisuchids *Susisuchus* and *Isisfordia* to be paraphyletic within an unnamed clade com-

prised of all potential hylaeochampsids (Schwarz *et al.* 2017). The symphyseal region of the mandible of *Susisuchus* is labiolingually expanded, which differs from NMS G.2016.21.1 (Salisbury *et al.* 2003). The dentary of *Isisfordia* cannot be compared with NMS G.2016.21.1, due to the holotype lacking the anterior region (Salisbury *et al.* 2006; Fortier & Schultz 2009).

Curiously, NMS G.2016.21.1 is most similar to two species of putative hylaeochampsids (Turner 2015): *Pachycheilosuchus trinquei* from the Early Cretaceous of Texas, USA (Rogers 2003) and *Pietraroiasuchus ormezzanoi* from the Early Cretaceous of Italy (specimen PC-1 in Buscalioni *et al.* 2011). The Skye jaw (NMS G.2016.21.1) shares with *Pachycheilosuchus* and *Pietraroiasuchus* a short mandibular symphysis, extending to the anterior border of the 4th alveolus (Figs 5, 6C–F). All three of the taxa have mild heterodont dentition and lack caniniform tooth (inferred for NMS G.2016.21.1 by the absence of any greatly enlarged alveoli). The Skye jaw is similar to *Pietraroiasuchus* in the gently arcuate form of the arcade in dorsal view, and in

that the splenial does not contribute to the symphyseal area (Buscalioni *et al.* 2011). In particular, the Skye jaw shares with *Pachycheilosuchus* a row of evenly spaced and ventrally positioned neurovascular foramina on the lateral surface of the dentary, which is a unique feature among hylaeochampsids (Fig. 6A–B). However, NMS G.2016.21.1 cannot be assigned to either of the two above genera. It is different from *Pietraroiasuchus* in the medially expanded anterior occlusal shelf in the latter (Buscalioni *et al.* 2011). In comparison with NMS G.2016.21.1, most small-bodied neosuchians display varying degrees of labiolingual expansion at the anterior tip of the dentary (Young *et al.* 2014, fig. 8; Young *et al.* 2016a, fig. 3; Fig. 5C). The dentary of *Pachycheilosuchus* has a small lingual projection along the symphyseal suture (Fig. 6D), but the anterior tip of the dentary is less labiolingually compressed than that in the Skye jaw (Fig. 5A–B).

4.1. Impact of ontogeny on assessment of NMS G.2016.21.1

The uncertainty of the ontogenetic stage of NMS G.2016.21.1 makes assessing its phylogenetic position problematic. Characters that unite NMS G.2016.21.1 with *Pachycheilosuchus*, the lack of dentary ornamentation and the shallow articulation rugosities in the symphyseal plate, are known to vary during ontogeny. In extant crocodylians, young individuals have shallow dermatocranial ornamentations that develop into prominent pits and rugosities in adults (Mook 1921; Joffe 1967). But lack of ornamentation may also imply a phylogenetic signal. Several fossil crocodyliforms represented by mature specimens have a smooth or weakly pitted external surface of the dentary. These include several "protosuchian" species (Yang 1973; Wu *et al.* 1997; Pol & Norell 2004a, b), various metriorhynchid genera (e.g., Young *et al.* 2013), the atoposaurid *Alligatorium* (Tennant & Mannion 2014), and *Pachycheilosuchus* (Rogers 2003).

Similarly, shallow rugosities in the symphyseal plate of NMS G.2016.21.1 may be phylogenetically informative, but these rugosities become deeper through ontogeny in extant crocodylians (Fig. 4). The dominant articulation type in Mesoeucrocodylia is Class III symphysis with interdigitated rugosities (Holliday & Nesbitt 2013), which is lacking in *Pachycheilosuchus* and NMS G.2016.21.1 (Fig. 6F). The latter two taxa have Class II articulation with shallow rugosities. The uncertain developmental stage of NMS G.2016.21.1 considered, these observations add information to "typical" symphyseal morphology in Neosuchia and potentially more inclusive clades in Crocodyliformes.

The lingual projection of the symphyseal suture remains reasonably stable throughout the ontogeny of extant crocodylians, which we observed in the lower jaw of *Alligator mississippiensis* (Fig. 4). It retains a labiolingual expansion near the anterior tip of the symphyseal suture, from hatchling-sized juveniles (AMNH R7129; Fig. 4A–B) to medium-sized young individuals (AMNH R7140; Fig. 4C–D), and into skeletal maturity (AMNH R66645; Fig. 4E–F). If *Alligator* is a good model for the ontogeny of the taxon NMS G.2016.21.1 belongs to, this indicates that the mediolateral constriction of the symphyseal suture observed in NMS G.2016.21.1 may not be an ephemeral juvenile feature, but may also be present in adult individuals; and, therefore, could be potentially diagnostic of a new taxon.

Based on the above comparisons, NMS G.2016.21.1 shares multiple mandibular characteristics with *Pachycheilosuchus* and *Pietraroiasuchus*, but its unique symphyseal region differs from all other neosuchians compared herein. We do not name a new taxon, given the incomplete nature of the specimen and

its likely juvenile status. Additional skull material and further understanding of ontogenetic changes in crocodyliform mandibles will help assess the phylogenetic position of NMS G.2016.21.1.

5. Discussion

Neosuchia *cf*. Hylaeochampsidae (NMS G.2016.21.1) is the first known definitive crocodyliform from the Duntulm Formation, which extends our knowledge of the Middle Jurassic archosaur assemblage of the Isle of Skye (Clark *et al.* 1995; Evans *et al.* 2006; Evans & Waldman 1996; Wills *et al.* 2014; Brusatte & Clark 2015; Brusatte *et al.* 2016; Young *et al.* 2016a). This specimen differs from other crocodyliforms currently known from Skye, including *Theriosuchus* sp. (Young *et al.* 2016a) from the Valtos Formation (Fig. 1A). *Theriosuchus* sp. has deep dentary ornamentation, strongly heterodont alveoli and a unique "starburst" morphology in the mandibular symphysis (NMS G.2014.52.1: Young *et al.* 2016a; Fig. 2D), none of which are present in NMS G.2016.21.1. Isolated neosuchian remains are also known from the Kilmaluag Formation that is stratigraphically immediately above the Duntulm Formation (Evans & Waldman 1996; Evans *et al.* 2006; Wills *et al.* 2014). The Kilmaluag material – comprising teeth, osteoderms and incomplete postcranial skeletons – is not directly comparable with NMS G.2016.21.1 due to lack of overlapping skeletal elements. It is possible that these specimens belong to the same taxon as NMS G.2016.21.1 and, if so, one or more of them would make more suitable holotypes, which is one reason we do not name NMS G.2016.21.1 here. These Kilmaluag specimens are currently under study, so their systematics and relationships with NMS G.2016.21.1 will become clearer in the future. These discoveries show that there were various small-sized neosuchians in the nearshore ecosystems of the Isle of Skye during the Middle Jurassic.

5.1. Implications of NMS G.2016.21.1 as a potential hylaeochampsid

The morphological resemblance of NMS G.2016.21.1 to *Pachycheilosuchus* and *Pietraroiasuchus* could potentially have implications for the evolution of Hylaeochampsidae that currently is only known from the Cretaceous (Norell & Clark 1990; Pol *et al.* 2009; Turner 2015). Should *Pachycheilosuchus* and *Pietraroiasuchus* be referred to Hylaeochampsidae, then NMS G.2016.21.1 would suggest this clade has a much longer evolutionary history than previously known. The type species *Hylaeochampsa vectiana* is known from the Early Cretaceous of the Isle of Wight (southern coast of the United Kingdom), whilst all other species consistently referred to Hylaeochampsidae are known from the Late Cretaceous of Europe (Clark & Norell 1992; Martin 2007; Delfino *et al.* 2008a, b; Puértolas-Pascual *et al.* 2014). Therefore, NMS G.2016.21.1 potentially could extend the temporal range of Hylaeochampsidae, or a slightly more inclusive clade, into the Middle Jurassic, and geographically into the north of the United Kingdom.

However, it is possible that NMS G.2016.21.1, *Pachycheilosuchus* and *Pietraroiasuchus* form a clade of derived neosuchians that are basal to Eusuchia. The variable phylogenetic position of *Pachycheilosuchus* is one of the biggest issues in determining where NMS G.2016.21.1 belongs on the crocodyliform tree, second only to the specimen's general incompleteness. *Pachycheilosuchus* was originally described as a possible atoposaurid (Rogers 2003), but Turner (2015) recovered it at the base of Eusuchia. Other studies have recovered this species in radically different positions, such as: in a more basal position within Neosuchia, closer to the split with Tethysuchia

(Adams 2014); as a derived neosuchian but basal to Eusuchia (Narváez *et al.* 2015); as a basal neosuchian, even more basal than the Tethysuchia–Eusuchia split (Tennant *et al.* 2016b); or in a clade with an assortment of hylaeochampsids and susisuchids (Schwarz *et al.* 2017). The phylogeny of Turner (2015) is consistent with Buscalioni *et al.* (2011) in the monophyly of Hylaeochampsidae, despite the fact that the latter study found *Pietraroiasuchus* as the sister group of *Pachycheilosuchus* (although they did not sample *Acynodon*). Young *et al.* (2016b) recovered *Pachycheilosuchus* and *Pietraroiasuchus* as sister taxa, and that clade was the sister taxon to Crocodylia. However, Young *et al.* (2016b) did not sample any other hylaeochampsids.

The incompleteness of NMS G.2016.21.1 hinders its inclusion into a rigorous phylogenetic analysis of Hylaeochampsidae, but new dentary characters are observed in multiple putative members of the clade and will be important in future systematic evaluations. The mandibular symphysis extends less than four alveoli in NMS G.2016.21.1, *Pachycheilosuchus* (Rogers 2003) and *Pietraroiasuchus* (Buscalioni *et al.* 2011), and it is shorter than five alveoli in *Acynodon iberoccitanus* (Martin 2007). In all these taxa, the dentary alveoli extend no deeper than the dorsal margin of the Meckelian canal. These characters could potentially be diagnostic of Hylaeochampsidae.

Several clades of small-to-medium-sized Mesozoic neosuchians have been suggested to be closely positioned to the origin of Eusuchia, including Hylaeochampsidae, Susisuchidae, Bernissartiidae and Paralligatoridae, although the taxonomic compositions of these clades vary among crocodyliform phylogenies (e.g., Turner & Sertich 2010; Adams 2014; Turner 2015; Young *et al.* 2016b; Schwarz *et al.* 2017). However, the various phylogenetic analyses appear to converge on a divergence between the large-bodied and primarily aquatic neosuchian clades (Pholidosauridae + Dyrosauridae) and the relatively smaller-bodied, terrestrial or semi-aquatic clades (although the position of Goniopholididae is variable; Adams 2014; Turner 2015; Young *et al.* 2016b; Schwarz *et al.* 2017). Yet little is known about neosuchians before the Late Jurassic due to a patchy non-marine fossil record (Mannion *et al.* 2015; Tennant *et al.* 2016b). The earliest definitive record of pholidosaurid material comes from the Late Jurassic of Uruguay and France (Fortier *et al.* 2011). The Bathonian age for the putative pholidosaurid *Anglosuchus* was questioned by Watson (1911), and the specimens referred to this taxon cannot be located.

Discovery of a specimen morphologically similar to putative hylaeochampsids from the Middle Jurassic suggests that small body size, which is widespread among basal eusuchians, emerged early in Neosuchia. We remain cautious in this conclusion, however, because an accurate estimate of adult body size of NMS G.2016.21.1 cannot be determined due to its incomplete nature and likely juvenile status. Further investigation is required to elucidate the distribution, mode and magnitude of body size evolution among advanced neosuchians, and we suggest that the discovery of new Middle Jurassic fossils from places like the Isle of Skye may hold the key.

6. Conclusion

The new lower jaw from the Isle of Skye helps shed light on the evolution of crocodyliforms during the mysterious Middle Jurassic interval. Whilst it has several distinctive dentary characters, particularly in relation to the Meckelian canal and mandibular symphysis, we do not refer it to a new taxon due to its incompleteness. Based on similarities in the mandibular symphyseal suture and dentary alveoli, this specimen appears to have an affinity with the Early Cretaceous putative hylaeo-

champsids *Pachycheilosuchus trinquei* and *Pietraroiasuchus ormezzanoi*. Furthermore, the anterior dentary and alveolar morphological variation described herein will hopefully contribute to future phylogenetic analyses, especially those including taxa referred to Hylaeochampsidae. Along with other discoveries from Skye, this new specimen shows that small-bodied neosuchians were diversifying in the Middle Jurassic, during a time when their fossil record is extremely poor.

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